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THE INHERITANCE OF CHARACTERS IN RICE, I

BY

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I. INTRODUCTION.

THE existence of an extraordinarily large number of well marked varieties is a striking feature of cultivated rice. It would be possible to collect many thousands of differently named varieties cultivated in India. Many of these are probably identical, though bearing different names, whereas in many cases the same name is applied to several different varieties. It is probable that the genetically distinct varieties would number several thousands.

The characters in which the varieties differ from each other are extremely varied. On the one hand are morphological characters affecting the colour, size, shape, etc., of various parts of the plant; on the other hand are such physiological characters as determine water-requirement, length of duration, vigour, etc. The variations shown in some of these characters are described by several authors who have proposed systems of classification of rice. The most recent work of this nature is by Graham[1] in India and Kikkawa[2] in Japan.

The present paper deals with the method of inheritance of some of the simpler characters. The material from which the results were obtained

[1] Graham, R. J. D., *Mem. Dept. of Agr. in India, Bot. Series*, vol. VI, no. 7.
[2] Kikkawa, S., *Journal of the College of Agr., Imperial University, Tokio*, III, 2.

consisted very largely of natural crosses resulting from the cultivation, side by side, of a large number of different varieties.

In 1913, when this work was started, an examination was made of about one hundred varieties growing on the Government Farm at Coimbatore. Some of these were almost pure, containing very few plants differing from the type, whereas others were so much mixed that it was impossible to distinguish a definite type for the variety. In each variety a few type plants were selected, together with any variations which were to be found. In selecting the latter such plants as appeared to be unrelated to the type, due to accidental mixture of other varieties, were neglected.

Almost all these selected plants were selfed in the manner described below. Their progeny, grown in 1914, showed that a large proportion of the aberrant plants were heterozygous. The segregating families gave Mendelian ratios for various characters and these were followed up in further generations. For the sake of convenience the original aberrant plants which proved to be heterozygous will be referred to as F_1 and their progeny as F_2, F_3, etc.

In addition to this material a few definite crosses were made between pure strains.

II. PRELIMINARY CONSIDERATIONS.

(*a*) Pollination.

From the accounts published by observers in different places it would seem that the details of normal pollination vary considerably for different localities.

Knuth[1] states that dehiscence of the anthers does not take place till they are fully extended and in a pendent position. Akemine[2] has found that in a variety of North Japan self-fertilization takes place immediately before the flowers open. Fruwirth and Van der Stok[3] conclude that in Java cross-fertilization occasionally takes place between neighbouring plants.

Farneti[4] reports that in Italy rice is cleistogamous, the glumes remaining closed throughout flowering. A number of freshly introduced and old acclimatized varieties gave the same result and he concludes that cross-fertilization is impossible.

[1] Knuth, P., *Hand-book of Flower Pollination*, vol. III, 1909, page 521.

[2] Akemine, M., "Ueber die Blute und das Bluhen von *Oryza sativa*," *Landw. Ztsch. Nogyo-Sekai*, 1910-11.

[3] Fruwirth, C., and Van der Stok, E., *Die Zuchtung der Landw. Kulturpflanzen*, Bd. V, p. 36.

[4] Farneti, Rodolfo, *Atti dell Istituto Botanico dell Universita di Pavia, Series II*, vol. XII, 1913, p. 351.

Hector[1], working in Lower Bengal, finds that dehiscence of the anthers normally takes place at the moment of opening of the glumes whilst the stigmas are still enclosed. He estimates, provisionally, that cross-fertilization may take place to the extent of about 4 per cent.

Graham[2] states that in five years' work at Nagpur, during which many different varieties were grown in adjacent lines, no case of natural crossing was detected.

McKerral[3] shows that in Lower Burma a certain amount of crossing undoubtedly takes place. His figures in connexion with the crossing of white rice by red (*l. c.* p. 326) indicate about 4 per cent. of total cross-fertilization.

Thompstone[4] notes that in Upper Burma "pollination takes place before the glumes open, or at the moment of opening—seldom afterwards." He finds that " .... hybrids are quite common among the numerous rogues to be found in nearly every field of ordinary paddy ...."

Observations made at several places in the Madras Presidency show that there is some difference between different varieties. Most commonly dehiscence does not take place till the glumes are well open and the anthers are partially extruded. Very exceptionally dehiscence takes place immediately before or during the opening of the glumes, whereas occasionally it is postponed till some seconds after the anthers have assumed a pendent position. In some cases it has been found possible to perform successful emasculations, for crossing purposes, by allowing the glumes to open naturally and removing the anthers as they emerge.

The amount of cross-fertilization taking place naturally was estimated for several varieties. In each case a variety was chosen which normally possessed a purple tip to the grain, but in which occasional plants altogether lacking in purple colouring were to be found. It will be seen later that such green plants are pure recessives, so that any purple-tipped plants in their progeny must be due to crossing. A few of these pure green plants, surrounded by the purple-tipped type, were picked out and allowed to set seed naturally. Their progeny contained a small number of purple-tipped plants which were counted and calculated as a percentage of the total number as shown in Table I.

[1] Hector, G. P., *Mem. Dept. of Agr. in India, Bot. Series*, vol. VI, no. 1.
[2] Graham, R. J. D., *l. c.*, p. 214.
[3] McKerral, A., *Agr. Jl. India*, vol. VIII, 1913, p. 317.
[4] Thompstone, E., *Agr. Jl. India*, vol. X, 1915, p. 26.

TABLE I.

Amount of natural cross-fertilization.

Variety	District	Total progeny	Purple-tipped crosses	Per cent. crossing
Sadai Samba	Coimbatore	2,491	72	2·9
Dodda Biru Bhatta	do.	2,019	2	0·1
Swarnawari	do.	2,039	18	0·9
Do.	South Arcot	2,888	20	0·7
Rasangi	Godaveri	3,794	92	2·4
Rascadam (1)	Coimbatore	1,435	21	1·5
Do. (2)	do.	3,350	46	1·4

It appears that the amount of crossing varies considerably with the variety, as would be expected from the variation in time of dehiscence of the anthers.

The last two lines of the table show the amount of crossing taking place between two varieties growing on adjacent plots. No. (1) represents 50 heads of *Rascadam* taken from the line of contact, that is actually commingling, with another variety. No. (2) represents 50 heads taken at a distance of three feet from the line of contact. That the amount of crossing is practically the same for both is no doubt due to the fact that the prevalent wind, which is fairly constant at the time of flowering, was blowing towards the *Rascadam* from the other variety. Further experiments are necessary to determine the amount of crossing taking place over greater distances.

(*b*) METHOD OF SELFING.

The method of selfing adopted has been to cover the entire upper portion of the plant with a bag made of fine mull. The bag reaches from well above the fully developed heads down far enough to include the tops of young tillers in shot blade. The latter can thus grow up into the bag before the panicle emerges. In this way the whole of the flowers are selfed, with the exception of such already set flowers as have to be removed at the time of bagging.

The bag is supported inside by two bamboo stakes standing vertically, one on each side of the plant, to a height a little above that of the developed panicles. It is closed loosely at the bottom by means of a pin on each side between the bamboos and the plant.

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The setting inside such a bag is perfectly normal and the bag may be left on till harvest when it is tied tightly round the bottom, after removing the bamboos, and the whole plant is pulled up and dried.

This method of selfing has proved very satisfactory, requiring little labour and causing no loss of seed. Only in one or two cases, out of a very large number of plants, have wrong types appeared which may have been due to crossing. It is possible, though not certain, that these were due to accidents of another nature.

Waterproof paper bags, one over each head, were tried, but, in spite of liberal ventilating holes, the moist atmosphere developed inside very seriously interfered with setting.

In all cases where the progeny of an unselfed plant are included in a table this fact is indicated by the letter "N" after the reference number of the parent. Such plants have been used freely in tables for simple ratios where a small amount of crossing would only slightly affect the ratio.

III. CHARACTERS INVESTIGATED.

(*a*) Size of outer glumes.

The spikelet of rice is single flowered and possesses two outer or sterile glumes, an inner fertile glume and a palea. In all references to the spikelet, the *outer glumes* will be referred to as such. The fertile glume and palea are hooked together at their edges to form one common structure, the husk; they are of similar texture and appearance and are affected by the same characters and will, therefore, be referred to together as *inner glumes*.

The outer glumes are usually small and inconspicuous, about $\frac{1}{4}$ to $\frac{1}{5}$ the length of the inner glumes (Plate I, figs. 2-6). In one of the varieties growing at Coimbatore, *Rakki Pakshi Bhatta*, the outer glumes are approximately equal in length to the inner glumes (Plate I, fig. 1). In India this character appears to be met with in only a few rare varieties in different parts.

In a plot of a short-glumed variety, which was showing considerable variation due to previous crossing, several long-glumed plants were found. Eight of these plants were selected and their progeny, though showing segregation for other characters, were all pure long-glumed. On the other hand, of the short-glumed plants from the same plot, selected for variations in other characters, several gave families showing segregation for this character. There were two very definite groups, *short-glumed* and *long-glumed*, in the ratio of about 3 : 1 respectively. The individuals of the dominant group were all typically short-glumed with no distinction between heterozygotes and

homozygotes. The long-glumed recessives were rather variable, but in no case did they approach the other group.

A number of F_2 plants from two segregating families gave the following results in F_3:—

7 long-glumed F_2 plants gave pure long-glumed F_3.

20 short-glumed ,, ,, { 7 pure short-glumed F_3. / 13 segregating F_3.

From the figures given in Table II it is evident that the normal *short-glumed* character is simply dominant to the *long-glumed*.

This is in accordance with the results of Van der Stok[1] who states that the normal type is dominant.

TABLE II.

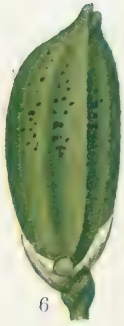
Length of outer glumes.

Origin of parent	Reference No.	Short-glumed	Long-glumed
Natural crosses	45	96	35
	131-N	74	26
	166	75	19
	169	19	6
	637	258	126
No. 45. F_2	four plants short-glumed	1,101	360
No. 637. F_2	eight plants short-glumed	7,034	2,324
Total ..	....	8,657	2,896
Calculated 3 : 1 ..		*8,664·75* :	*2,888·25*

(*b*) GOLDEN COLOUR OF INNER GLUMES AND INTERNODE.

The most usual colour of the inner glumes is a light green (Plate II, fig. 1) ripening to pale straw, but there are numberless varieties with other colours. Of these one of the commonest is some form of what may be described as *golden* colouring, though this varies in different varieties from orange-yellow to reddish-brown (Plate II, figs. 2 and 3) at the time of flowering, becoming rather darker and duller on ripening. Plate I shows photographs of ripe grains of green (fig. 2) and gold (figs. 1 and 3.)

[1] Van der Stok, *l. c.*, p. 47.



COLOURS OF INNER GLUMES.

1. Ordinary green, "Sadai Samba."
2. Light gold, "Sakalati Sanna Bhatta."
3. Dark gold, "Ottadan.
4. Dark furrows, "Pisini."
5. do. piebald, } "Manawari."
6. do. do. }

7

8

9

10

11

12

COLOURS OF INNER GLUMES.

7. Gold piebald, "Garudan Samba."
8. Green,
9. Gold,
10. Patchy gold (one panicle)
11. Patchy gold (one panicle)
12. Patchy gold (one panicle)

from No. 432, F_2

In plants with golden inner glumes the internode is golden, whereas a light green internode normally accompanies green glumes. In all the material so far examined, with the exception of one family to be described later, this connexion between the golden colour of inner glumes and internode has been constant. It will be seen later that purple colouring of inner glumes and internode depends on two separate factors which may be coupled so closely as to appear as one factor. Whether this is the case with golden colouring remains to be seen from future work.

The golden character, irrespective of the actual shade of colouring, behaves as a simple recessive to green. The total available figures are given in Table III which shows a simple *3 : 1* ratio of *green* to *gold*.

Thompstone[1] describes a *3 : 1* ratio of *white* : *deep rusty-red* which is presumably the same as the above *green* and *gold*.

TABLE III.

Golden colouring of inner glumes and internode.

Origin of parent	Reference No.	Green	Gold
Natural cross	10	219	80
No. 10, F_2	446–N	173	60
	455–N	377	119
Natural cross	178	447	161
No. 178, F_2	589–N	300	92
Green crosses from unbagged golden plants ..	540–N	944	378
	543–N	808	266
	544–N	362	118
	657–N	828	276
From F_2 not counted	563–N	157	49
	566–N	284	73
	574–N	229	62
Total of 17 other families ..	....	3,436	1,155
Total ..	....	8,564	2,889
Calculated 3 : 1 ..		*8,589·75*	*: 2,863·25*

[1] Thompstone, E., *l. c.*, p. 45.

All the greens are the same with no difference between heterozygotes and homozygotes. In all the above families the type of golden colouring has been uniform in each family but varying in different families.

On the presence and absence hypothesis an inhibitory factor must be responsible for the failure to develop golden colouring in the above families. It is possible that the actual production of this colouring is dependent on the presence of a factor which may vary for the different types of colouring. In this case it must be assumed that all these families were pure for one or more such factors. No definite proof of the existence of such factors has so far been obtained but there is some indication of this in certain complicated families in which different types of golden colouring occur together.

In one such family, which was not giving the ordinary 3 : 1 ratio, two distinct types of gold were present. The F_1 parent, which possessed light golden inner glumes and internode, gave very few plants in F_2. Of these the inner glumes varied from green to dark gold with various intermediates ; a rough analysis showed *green* 9, *light gold* 9, *dark gold* 5. All internodes were golden and this character has been pure in the further generations. Four of these F_2 plants gave glume characters in F_3 as shown in Table IV.

TABLE IV.

Reference No.	Character of parent	Green	Patchy-gold	Gold	Ripening gold
429-N .. .	Green	2,545	..	..	
431-N	do.	1,208	..	..	357
432-N	Light gold	597	1,292	592	.
430-N ..	Dark gold	..	..	1,118	..

In all plants described as green the glumes were distinctly yellowish as compared with typical greens but they ripened to the ordinary straw colour.

In No. 431-N the ripening gold group could be distinguished only with difficulty at flowering, but, as the grain developed, the colour became more pronounced till at maturity it was a definite dull gold of a rather light shade. All unset grains remained green whereas in ordinary gold types unset grains are definitely gold though they fail to darken with age. Table V gives the results of a further generation from this family.

TABLE V.

Origin of parent	Reference No.	Character of parent	Green	Ripening gold
No. 3, F$_2$	431–N	Green	1,208	357
	742–N	Ripening gold	..	all
	743–N	do.	..	all
	744–N	Green	all	..
No. 431–N, F$_3$	745–N	do.	1,421	525
	746–N	do.	all	..
	747–N	do.	993	279
Total segregating ..	..	..	3,622	1,155
Calculated 3 : 1 .	..	..	*3,582·75* .	*1,194·25*

The figures show an obvious *3 : 1* ratio, similar to that of Table III, and it appears that a somewhat similar inhibitory factor may be concerned. If so, this factor differs from that already described in that it has no effect on the internode and the inhibition in the glumes is not complete since, as already noticed, they possess a distinctly yellowish tinge. It may be noted that in some of the families concerned one or two plants occurred in which both glumes and internode were entirely green. These must have been natural crosses from outside as they also varied from the group in certain other characters. There is little doubt that they possess the ordinary inhibitory factor, crossed on from another group, and their progeny will be of interest in their connexion.

To return to Table IV, in No. 432-N, three groups appeared, *viz.*, *green*, *patchy-gold* and *gold*, in the approximate ratio of *1 : 2 : 1*. These groups, which are shown in Plate II, figs. 8-12, were distinct and easily separable. The greens were of the same yellowish type as has already been described and the golds were of an ordinary medium shade but with small green areas at the apex and base of the grain. In the patchy-golds the colouring varied considerably, both in shade and extent (Plate II, figs. 10-12) even on the same plant. It was always irregularly patchy and quite distinct from the piebald type (Plate II, fig. 1) which will be described later.

The results of a further generation are shown in Table VI.

TABLE VI.

Origin of parent	Reference No.	Character of parent	Green	Patchy-gold	Gold
No. 3, F_4	432–N	Light gold	597	1,292	592
	749–N	Green	all	..	..
	750–N	do.	all	..	..
	751–N	Gold	..	..	all
	752–N	do.	..	..	all
No. 432–N, F_3	753–N	Patchy-gold	287	675	282
	754–N	do.	286	604	288
	755–N	do.	74	231	78
	756–N	do.	76	172	82
Total segregating ..	..	..	1,320	2,974	1,322
Calculated 1 : 2 : 1 ..	..	..	*1,404* :	2,808 :	*1,404*

It is evident that the figures represent a *1 : 2 : 1* ratio and the patchy-golds apparently form a heterozygous group intermediate between homozygous greens and golds. It may be that this is due to an inhibitory factor incompletely dominant for this type of gold, or possibly no inhibitory factor is concerned but only an incompletely dominant gold-producing factor.

Since the families of Tables V and VI were derived originally from the same parent it is probable that the same inhibitory factor is concerned in both lots and that the difference in effect is due to the different gold-producing factors present. This supposition is supported by the fact that in one of the pure green families of Table V there occurred one typical patchy-gold plant which no doubt was a natural cross by a gold plant in No. 432 of Table VI which was growing in the vicinity. Moreover in the pure green families of Table VI there occurred one or two obvious crosses with entirely green glumes and internode, due undoubtedly to the introduction of the ordinary inhibitory factor from outside as has been already described for similar crosses in families of Table V.

(*c*) DARK FURROWS OF INNER GLUMES.

In this character a dark blackish-brown colour develops in the inner glumes, more especially in the furrows (Plate I, fig. 4 and Plate II, fig. 4).

It begins to appear at about flowering time, increases in intensity as the grain develops, and then fades to a dull brown during the later stages of ripening.

It was at first thought that an inhibitory factor, similar to that described for golden colouring, existed for this character also. Numerous figures were obtained showing a *3 : 1* ratio of *green* to *dark furrows*. It now appears likely that the greens were not in reality entirely green but that the colour was limited by the *piebald* factor described below.

Since the action of this factor was noted all families apparently segregating into greens and dark furrows have been examined carefully and in every case the *greens* have proved to be in reality *piebald dark furrows*. It is recorded for some of the earlier lots that the greens were not entirely devoid of colouring and these no doubt were really piebalds. It is not certain, however, that this was true in all cases.

Many varieties exist in which the glumes are entirely free from this colouring, but whether this is due to the absence of the determining factor or to the presence of an inhibitory factor remains to be seen from future work.

(*d*) Piebald pattern of golden colouring and dark furrows of inner glumes.

There is a definite localization factor which affects the distribution of both ordinary golden colouring and dark furrows of the inner glumes. This was first noted in golden types where the colour is inhibited at the base of the glumes, typically to about one-third of the length, and also in a small area at the apex. There is often considerable variation, even in grains on the same head, but the character on the whole gives the very definite *piebald* appearance of the grain which is common in many varieties (Plate I, fig. 5 and Plate II, fig. 7).

Reference has already been made to this factor in connexion with dark furrows. Here the effect is extremely irregular in segregating families and even in varieties pure for this character considerable variation exists. The minimum of inhibition corresponds roughly with typical gold piebald (Plate I, figs. 5 and 6 and Plate II, figs. 5 and 7). This amount of colouring is generally seen in occasional plants only and, even there, is often confined to a few of the upper grains in the panicle. From this all stages may be found down to those in which a careful search reveals, on a whole plant, only a few grains in which a few specks of colour are present. An ordinary typical *piebald dark furrows* plant exhibits about the amount of colouring shown in Plate II, fig. 6, on a number of grains in each panicle.

The *piebald* character is dominant to *self-colour*, giving the ordinary *3 : 1* ratio in F_2 (*see* Table VII). It has not yet been ascertained whether the

variation noted as existing in the piebalds is to any extent dependent on the heterozygosis or otherwise of the localization factor.

TABLE VII.

Piebald localization factor.

Origin of parent	Reference No.	Dark Furrows		Golden	
		Piebald	Self-colour	Piebald	Self-colour
Natural cross	47	25	8	12	7
No. 47, F_2	504	..	..	177	55
	505	..	..	121	44
	506	39	16	..	..
	507	111	39	39	21
	508	..	..	40	12
Natural crosses	166	55	19	15	5
	626	340	147	101	42
	217	..	..	180	63
No. 639, F_2, not counted ..	1,003–N	1,250	390	..	..
	1,004–N	1,304	433	..	..
	1,007–N	766	233	..	..
	1,009–N	1,082	330	..	..
Total ..	..	4,972	1,615		
Calculated 3 : 1 ..	..	*4,940·25 :*	*1,646·75*		
	Total ..	..		685	249
	Calculated 3 : 1 ..			*700·5 :*	*233·5*

There can be no doubt that the same factor is concerned in both types of colouring though the numbers illustrating this are not very good approximations to a *9 : 3 : 3 : 1* ratio.

(*e*) PURPLE PIGMENTATION.

The occurrence of anthocyan pigmentation in some part of the plant is extremely common and different localizations of this colouring form some of the most striking varietal characters.

The pigment, which occurs in solution in the cell-sap, will be referred to throughout as purple. The actual appearance, however, varies considerably

according to the concentration of the pigment and the colour of the tissue in which it is present. Thus in the epidermis of a dark green sheath it appears bluish, whereas in an otherwise colourless stigma it appears reddish when in low concentration and almost black when highly concentrated. In no case has the pigment itself appeared to show variation when examined under a lens.

The inheritance of several localization factors will be considered later; the factor at present under consideration is the power to produce purple pigment.

One of the commonest types of segregation in F_2 families from naturally occurring heterozygotes has been the production of pigmented and unpigmented plants. The former group has varied in the different families according to the localization factors present in each case.

Table VIII shows a few F_2 and F_3 families in which the ratio *pigmented : unpigmented* is *3 : 1*.

TABLE VIII.

Purple pigmentation, 3 : 1 *ratio*.

Origin of parent	Reference No.	Pigmented	Unpigmented
Natural cross	10	222	77
No. 10, F_2	437–N	1,276	361
	440–N	362	119
	441–N	1,093	360
Natural cross	640	211	66
No. 640, F_2	671–N	701	231
	673–N	1,064	56
	687–N	680	241
Total ..	..	5,609	1,811
Calculated 3 : 1 ..	.	*5,565* :	*1,855*

This ratio has been obtained in a large number of families, the totals for which are as follows :—

	Pigmented	*Unpigmented*
85 families F_2-F_4 ..	41,164	13,664
Calculated 3 : 1 ..	*41,121* :	*13,707*

In two F_2 families, however, a *9 : 7* ratio was obtained, and in each case both ratios, *9 : 7* and *3 : 1*, appeared in further generations as shown in

Table IX. In all cases several localization factors were present, some pure, others segregating, so that all plants capable of producing pigment must have possessed a localization factor.

TABLE IX.

Purple pigmentation, 9 : 7 *ratio.*

Origin of parent	Reference No.	Pigmented	Unpigmented	Ratio
Natural cross	178	345	263	9 : 6·9
No. 178, F_2	602–N	445	327	9 : 6·6
	589–N	*296*	*96*	*9 : 2·9*
	599–N	166	120	9 : 6·5
	605–N	*105*	*130*	*9 : 5·8*
Natural cross	190	40	30	9 : 6·75
No. 190, F_2	611–N	*762*	*204*	*9 : 2·4*
	614–N	817	602	9 : 6·6
No. 614–N, F_3	Ten families	*7,884*	*2,519*	*9 : 2·9*
	Six families	3,001	2,333	9 : 7·0
Total 3 : 1 ratios, distinguished by *italics* ..		9,247	2,949	
Calculated		*9,147*	: *3,049*	
Total 9 : 7 ratios ..		4,814	3,675	
Calculated ..		*4,775*	: *3,714*	

The figures for these families are sufficiently definite to leave no doubt that the formation of pigment is dependent on the simultaneous presence of two factors. It must be assumed that all the above families, giving a *3 : 1* ratio, were pure for one of these factors.*

Confirmatory evidence of the existence of two pigmentation factors has been obtained by the production of a pigmented plant by crossing two unpigmented types.

* *Note* :—Since this was written a paper has been published by Hector, "Observations on the Inheritance of Anthocyan Pigment in Paddy Varieties," *Mem. Dept. of Agr. in India, Bot. Series*, vol. VIII, no. 2.

He has obtained both *3 : 1* and *9 : 7* ratios of *pigmented* : *unpigmented*, the latter being more common. His interpretation of results differs from that adopted in the present paper in that no distinction is made between *pigmentation* and *localization* factors. Such a distinction would simplify the explanation of many of the results given; thus all the families of Table III, p. 94, might be considered to be segregating for two pigmentation factors and the stigma localization factor, but pure for the leaf-sheath and apiculus localization factors. [F. R. P.]

1 2 3 4

1. Ripening black
2. do. straw

} from No. 568, F_2.

3. Pulvinus and auricle dark purple
4. do. do. green

} from No. 456. F_2

PLATE III.

Six unpigmented F_3 plants, from No. 614-N of Table IX, were crossed with pollen from a pure unpigmented strain of *Garudan Samba*. One cross gave two plants one of which was pigmented whereas the other was not. In the other five lots, comprising 13 plants, all were unpigmented.

(*f*) Dark purple colouring of pulvinus and auricle.

In this character a very dark purple colouring of the epidermis is present in the pulvinus and also in the auricle and pulvinus-like region from which it springs at the junction of leaf-sheath and lamina (Plate III, fig. 3). The term *pulvinus* is applied to the swollen growth zone at the base of the leaf-sheath immediately above the node. The pigment is so concentrated as to appear black unless closely examined.

In all cases so far noted the two localizations have gone strictly together, forming a single character which is dominant to the unpigmented type. It is probable that a single factor is concerned though it might be a case of complete coupling of two separate factors.

The figures given in Table X show, approximately, a simple *3 : 1* ratio. There is some variation in the pigmented group which is possibly due to the heterozygotes being less evenly coloured. This is a matter more of distribution of pigmented cells than of concentration of pigment in the cell.

Table X.

Dark purple colouring of pulvinus and auricle.

Origin of parent	Reference No.	Pigmented	Unpigmented
Natural cross	10	175	48
No. 10, F_2	437	971	305
	439-N	476	140
	442-N	695	182
	453-N	226	74
Natural crosses	11	61	22
	86	190	58
Total		2,794	829
Calculated 3 : 1		*2,717·25* :	*905·75*

(*g*) Full-purple self-colour of leaf-sheath.

In this character the epidermis of the leaf-sheath is coloured very distinctly purple, especially in the sides and edges. The colouring, although frequently

most intense in the lower half of the sheath, always extends up to the junction with the lamina and often into the ligule. The lower sheaths, especially such as are poorly developed, show the maximum amount of colouring.

Plate IV shows two types which were crossed, B, 1 possessing this character and B, 23 in which, although some purple colouring appeared in the sheath, this definite character was absent. The purple lining of the sheath and internode of B, 1 is due to a separate factor, to be considered later, which is in no way connected with that under consideration.

Six F_1 plants were obtained from this cross, all with full-purple sheaths. In F_2 a simple *3 : 1* ratio was obtained for presence and absence respectively of full-purple. In the latter group some individuals were practically devoid of self-colour, whereas others reproduced the small amount shown by B, 23. It was found that this colouring in B, 23 was almost entirely due to a separate character, to be described later as *purple axil*, mainly affecting the colour of the inside surface of the sheath. This was absent in B, 1 ; hence the F_2 was segregating for this character as noted. Certain families in F_3 again gave the *3 : 1* ratio for full-purple. Table XI gives the figures obtained with regard to this character only, leaving out of account other characters which do not affect it in any way.

TABLE XI.

Full-purple self-colour of leaf-sheath.

Origin of parent	Reference No.	Full-purple	Slight purple or green
F_1—B, 1 × B, 23	642	310	87
	643	304	111
	644	388	108
	645	138	47
	646	149	52
	647	344	91
No. 645, F_2	694–N	459	152
	696–N	420	145
	700–N	125	45
	703–N	615	236
	707–N	249	91
Total ..	..	3,501	1,165
Calculated 3 : 1 ..		*3,499·5* :	*1,166·5*

Type B, 1.—Full-purple self-colour leaf-sheath; purple lined sheath and internode; purple glumes; white stigma and axil.

Type B. 23.—Leaf-sheath full-purple absent; purple lining absent; green glumes; purple stigma and axil.

The full-purple character is obviously due to the presence of a simple factor, irrespective of any other colouring that may be present in the sheath. A good deal of variation in intensity of colouring exists in the dominant group and this proved to be partly due to the heterozygotes showing, on the whole, rather less colour than the pure dominants. The former could not be separated as a definite group, however, owing to the fact that varying exposure to light also affects the intensification of the colouring.

(*h*) Purple lining of internode, purple glumes, purple stigma, purple axil.

The above characters will be considered together, since, in certain crosses in which they were all concerned, several types of gametic reduplication occurred.

Purple lining of the internode is due to pigment in the sheaths of the vascular bundles. It is normally associated with a certain amount of lining in the leaf-sheath and it is possible that one factor determines both. It is a common character, found in very many varieties, and shows great variation. In some types the lining is faint and scarcely noticeable, developing only when the internode is exposed to strong light. Many intermediate forms exist between such types and those showing the fullest development where the whole internode is deeply coloured in shades varying from almost red to almost black.

Such deeply coloured types are included under purple lining as examination shows that the pigment is present mainly in the bundle sheaths, although it spreads into the surrounding cortex sufficiently to give the appearance of self-colouring.

There are undoubtedly several factors concerned in the various types of lining, but there appears to be considerable complication and they have not yet been worked out. So far as concerns the present considerations the actual type of lining is immaterial since all have behaved in the same manner.

The *purple glumes* character is somewhat variable. In all types noted the small outer glumes are almost entirely purple. The inner glumes vary, in the distribution of the colouring, from the type shown in Plate IV, B, 1, to one in which they are uniformly purple. The actual colouring also varies from ordinary purple to almost black.

The factors concerned in these variations have not been worked out, but, as in the case of purple lining, all types behave in the same manner in their relations considered below.

The type of *purple stigma* under consideration is shown in Plate IV, B, 23. Other types exist but are not included in this account.

The term *purple axil* is applied, for the sake of convenience, to a deep purple colouring of the epidermis on the inside of the sheath. It is most intense in the axil and gradually diminishes as it extends upwards till it disappears about half way up the sheath (Plate IV, B, 23).

As will be seen below, the above four characters behave as simple dominants to their respective unpigmented types, each character being due to the presence of a simple factor. In the following description the presence of these factors will be denoted by the capital letters L, G, S, A, respectively, and their absence by the corresponding small letters.

The principal material to be considered was derived from the cross between types B, 1 and B, 23 of Plate IV. Reference has already been made to this cross in connexion with purple self-colouring of the leaf-sheath ; this is entirely independent of the above characters and may be disregarded here.

These two types were plants from pure strains of the variety *Basangi*, separated by Mr. Hilson on the Government Farm at Samalkota. Their composition, together with that of F_1, may be represented as follows :—

B, 1	L L G G s s a a
B, 23	l l g g S S A A
F_1	L l G g S s A a

In F_2 it was found that each character, considered separately, behaved as a simple dominant, giving a *presence* : *absence* ratio of *3 : 1*. When all four characters were considered together it was found that :—

purple lining was associated with *purple glumes ;*
purple stigma „ „ *purple axil ;*
green internode and *glumes* were associated with *purple stigma* and *axil.*

Thus only three types occurred, which may be represented as L G s a L G S A and l g S A. The ratio approximated to *1 : 2 : 1* respectively, as shown by the figures in Table XII. It follows that—

L	is coupled with	G
S	„	„ A
L G	repels	S A

Thus the F_1 — L l G g S s A a — can form only two types of gamete, *viz.*, L G s a and l g S A, which result in the following ratio in F_2 :—

1, L L G G s s a a : *2*, L l G g S s A a : *1*, l l g g S S A A—*i.e.*, two pure types similar to the parents and a heterozygous type similar to F_1. This was confirmed in F_3 as will be seen from Table XII.

TABLE XII.

Type B. 1 × B. 23.

	Parents		L G s a	L G S A	l g S A	
F_1	6 plants ..	..	566	1,097	466	
F_2	23 plants, N. L G S A	..	6,969	14,070	7,242	*L g S A, 8* *l G S A, 11*
	Total ..	..	7,535	15,167	7,708	
	Calculated 1 : 2 : 1 ..		*7,602·5*	*15,205*	*7,602·5*	
F_2	8 plants, N. L G s a	..	2,750	..	..	
	8 plants, N. l g S A	..	..	..	5,622	

In the six F_2 families, totalling 2,129 plants, no case occurred in which L and G were not coupled. In the twenty-three splitting F_3 families, totalling 28,281 plants, nineteen showed failure of this coupling, as shown in italics in Table XII.

Unfortunately the F_2 parents of these families were not selfed and, therefore, it is not absolutely certain that these aberrant types were not crosses from outside the group. Crossing inside the group could only slightly affect the *1 : 2 : 1* ratio but could not produce the aberrant types.

A few undoubted cases of crossing from outside were found, but these were easily recognizable since the type of internode and glume colouring was quite distinct from that of the group, which was peculiar to itself.

The nineteen aberrant plants were absolutely typical of the group in all respects and there appears to be little doubt that they represent examples of incomplete coupling of L and G. It will be seen from tables that follow that occasional aberrant plants of these types are constantly occurring in families segregating for L and G and this fact supports the idea of incomplete coupling. To make quite certain of this point, and in order accurately to estimate the amount of coupling, fifty plants of the L G S A type have now been selfed. In view of this no further reference to this point will be made beyond giving the numbers of such aberrant types as occur in the families described.

No departure from complete coupling occurred with regard to purple stigma and axil.

The same set of characters appeared in No. 640, another cross with B, 23 but by an unknown male parent. F_1 was in appearance the same as the cross already described and its constitution proved to be the same, except that it was heterozygous for one of the pigmentation factors. Thus in F_2 *pigmented* and *unpigmented* plants appeared in the ratio of *3 : 1*. This did not affect the composition of the pigmented group, which was made up of the three groups already described — L G s a, L G S A and l g S A — in the *1 : 2 : 1* ratio. Here, again, in F_3 the same result was obtained. Six plants of the L G S A group all reproduced the *1 : 2 : 1* ratio, whereas six from each of the other groups all bred true (*see* Table XIII). No aberrant types were produced in this group.

TABLE XIII.

Parents	Reference No.	L G s a	L G S A	l g S A
F_1, B. 23 × ?	640	47	96	68
No. 640, F_2	6 plants, L G S A	731	1,702	879
Total	..	778	1,798	947
Calculated 1 : 2 : 1	..	880·75	1761·5	880·75
F_3	6 plants L G s a	2,824	..	..
	6 plants l g S A	..	..	4,014

N.B.—Unpigmented groups, occurring in certain of the above families, have been disregarded.

The above results are quite definite in showing repulsion between *purple lining and glumes coupled* on the one hand and *purple stigma and axil coupled* on the other. The exact nature of the repulsion, however, is not evident; thus either L, or G, or the L G combination, may repel either S, or A, or the S A combination. Some light is thrown on this point by another group of families arising from a naturally occurring heterozygote. This plant, No. 153, was a *rogue* with purple-lined internode and purple glumes in a variety, *Dalwa*, with green internode and glumes. F_2 was not counted but it was noted that segregation was taking place for purple lining and glumes, which were coupled, and that purple axil was pure. The stigma was not examined but from the

results given by F_3 it must have been segregating. Pigmented and unpigmented plants occurred in the ratio *3 : 1* in F_2; in F_3 and F_4 some families were pure and others impure for pigmentation. All unpigmented plants are disregarded in the following description.

The original rogue, referred to as F_1, must have been of the constitution L l G g S s A A—*i.e.*, the same as those described above with the exception of the pure purple axil. The results from F_3 and F_4, given in Table XIV below, show the same behaviour of the segregating factors. L and G are coupled in all but a few rare individuals, and repulsion takes place between LG and S.

As noted the stigma was not examined in F_2 but its nature in the F_2 parents selected can be deduced with certainty from their behaviour in F_3. The general behaviour of the whole group, neglecting unpigmented plants, was as follows :—

6 F_2 plants LGsA type bred true in 2,486 individuals.
7 F_3 ,, ,, ... 6,915 ,,
6 F_2 .. lgSA .. .. 2,916 ..
8 F_3 .. ,, ... 5,988 ..
6 F_2 .. LGSA ,, gave *1 : 2 : 1* ratio * } *see* Table XIV.
11 F_3 .. ,, ,, ,, }

TABLE XIV.

Origin of parent	Reference No.	L G s A	L G S A	l g S A	
No. 153, N, F_2 ..	553 N	104	227	97	*also L g S A, 1*
	557–N	98	214	108	
	560–N	135	268	156	
	568–N	49	96	48	.. *L g S A 1*
	570–N	132	250	125	
	571–N	102	173	116	
F_3	11 plants, N, L G S A	2,016	4,301	2,279	*L g S A, 1* / *l G S A, 1*
Total	..	2,636	5,529	2,929	
Calculated 1 : 2 : 1	..	*2,777 : 5,547 : 2,772.5*			
No. 190, F_2 ..	614–N	197	399	221	*also l G S A, 1*
No. 614, N, F_2 ..	8 plants, N, L G S A	1,471	2,960	1,504	.. *l G S A, 5* / *L g S A, 2*
Total	..	1,668	3,359	1,725	
Calculated 1 : 2 : 1	..	*1,688 : 3,376 : 1,688*			

* With very occasional aberrant types in addition.

The second half of Table XIV shows exactly similar results obtained in a totally unrelated group. The composition of No. 190, F_2, was not ascertained except that it was giving a *9 : 7* ratio of *pigmented* : *unpigmented* plants, in which connexion it has already been considered.

To return to the *Dalwa* cross, two F_2 plants of the L G S A type proved to be of the constitution L L G g S s A A. These may have been crosses, as the F_1 parent was not selfed, or they may have been due to failure of coupling of L and G. Their exact origin is immaterial to the present consideration *viz.*, repulsion between G and S where both L and A are pure.

The results given in F_3 and F_4 are shown in Table XV.

TABLE XV.

Origin of parent	Reference No.	L G s A	L G S A	L g S A
2 crosses in No. 153-N, F_4 ..	566-N	73	195	89
	577-N	77	230	144
No. 566-N, F_3	5 plants, N. L G S A	827	1,557	747
No. 577-N, F_3	6 plants, N. L G S A	1,018	2,249	1,242
Total	..	1,995	4,231	2,222
Calculated 1 : 2 : 1 ..	..	*2,087*	*4,174*	*2,087*

No explanation can be offered for the wide divergence of No. 577-N from the ordinary ratio, but it has been disregarded in view of the fact that the F_4 families show only a slight tendency to such divergence. The figures, on the whole, undoubtedly represent the ordinary *1 : 2 : 1* ratio, showing simple repulsion between G and S, with no complication due to coupling.

A similar example of simple repulsion, but this time between L and S, was furnished by an aberrant plant of the L g S A type arising from No. 568-N of Table XIV. The constitution of this plant appears to have been L l g g S s A A and simple repulsion between L and S resulted in the usual *1 : 2 : 1* ratio (Table XVI).

TABLE XVI.

Origin of parent	Reference No.	L g s A	L g S A	l g S A
No. 568-N, F_3	829-N	47	87	48
Calculated 1 : 2 : 1 ..	..	*45·5*	*91*	*45·5*

The results so far obtained show the following types of repulsion : -

L G repels S A
L G ,, S
G ,, S
L ,, S

Altogether over 60,000 plants have been examined with respect to the above types of repulsion and no example of incomplete repulsion has been recorded. It follows that the repulsion is at the least of an extremely high degree.

With regard to the coupling of purple stigma and purple axil the families showing segregation for both factors include about 34,000 plants but no failure of this coupling has been noted. This indicates that it is either complete or of a very high degree.

In this connexion it may be noted that purple stigma and axil are very commonly found associated with a purple tip to the inner glumes. This is a very well marked character (Plate IV, B, 23) quite distinct from the purple glumes already described. The above three characters are characteristic of a large number of varieties and there is evidence that they are also present in certain unpigmented varieties where the lack of a pigmentation factor prevents their appearance.

It is highly probable that the purple tip is coupled with the other two but no undoubted case has been noted. In the presence of purple glumes the tip cannot be determined ; thus the cross B, 1×B, 23 may have been either pure or impure for this factor. In the resulting families all plants with green internode and glumes possessed purple tips, showing that, if it was impure in the cross, this factor also was concerned in the reduplication already described.

It was at first thought that purple tip and stigma might be due to a single factor, since they invariably occurred together, but a few rare cases have now been found of purple tip associated with white stigma and *vice versâ*.

(*i*) Ripening black character of inner glumes.

In this character a black pigment appears in the inner glumes at the time when the fully developed grain begins to ripen. In one or two days the glumes become almost entirely black, with a slight brownish tinge, and the colour then fades considerably so that the grain, when dead ripe, has a dull smoky

appearance. The change takes place so rapidly that it is common to find faded smoky grains at the tips of the panicle before the lowest grains have developed the colour.

Plate III, figs. 1 and 2, show grains ripening *black* compared with others, from the same segregating family, ripening to the ordinary *straw* colour.

The results obtained show considerable complication and are not yet fully worked out. There is no doubt that two factors are concerned in the production of the black pigment and that segregating families may show *black : straw* ratios of *3 : 1* or *9 : 7* according as the parent is heterozygous for one or both of these factors.

Table XVII shows both ratios appearing in a group of F_4 families derived from an F_3 giving a *9 : 7* ratio.

TABLE XVII.

Origin of parent	Reference No.	Black	Straw	Ratio
No. 153-N, F_3, not counted ..	564-N	331	300	*9 : 8·1*
	813-N	359	86	*9 : 2·2*
	817-N	525	158	*9 : 2·7*
No. 564-N, F_3	815-N	246	197	*9 : 7·2*
	816-N	220	167	*9 : 6·8*
	818-N	309	280	*9 : 8·1*

There is little doubt that Nos. 813-N and 817-N represent *3 : 1* ratios, though the former is not a very near approximation, and that the other families represent *9 : 7* ratios.

The above families were pure for the absence of purple-lined internodes. They were segregating for a purple pigmentation factor which, however, did not affect the segregation for ripening black. In certain families, on the other hand, which were also segregating for purple lining in the internode, there was clear indication of gametic reduplication. It was not until much material had been destroyed, after making simple counts of *black* and *straw*, that this reduplication was noted, hence the internode character was not determined in many cases.

Table XVIII gives the figures for certain families segregating for purple lining in addition to *one* of the ripening black factors.

TABLE XVIII.

Reference No.	PL. Internode		G. Internode		Total	
	Black	Straw	Black	Straw	Black	Straw
825-N	189	83	88	3	277	86
851-N	673	339	348	10	1,021	349
849-N		695		6	524	177
Total ..		2,415		19	1,822	612
Partial repulsion, 3 : 1 type ..		2·96	:	3·8		
Partial repulsion, 7 : 1 type ..		2·124	:	9·5		
		Calculated 3 : 1	..		1,825·5 :	608·

The right side of the table shows that, in each family, the simple ratio of *black : straw* is *3 : 1*, due to segregation for a single factor. The figures on the left clearly indicate partial repulsion between this factor and the purple lining factor. Unfortunately in No. 849-N the full figures are not available since only the *straw* plants were examined with regard to internode. It is obvious, however, that in all three families the repulsion was approximately of the same degree.

The degree of repulsion is of interest since, as seen by the calculated figures, it is definitely intermediate between the two recognized reduplication ratios — *3 : 1* and *7 : 1*.*

When both ripening black factors are segregating it appears that both are subject to partial repulsion by the lining factor. The few families for which figures are available show considerable irregularity in their ratios, suggesting varying degrees of repulsion, but further results are necessary before a definite statement to this effect can be made.

It is of interest to notice that where both ripening black factors are subject to this partial repulsion they come together oftener than would otherwise be the case and the ordinary *9 : 7* ratio is upset. This explains certain irregular results that had been very puzzling before the cause was known. Thus from a family giving a *black : straw* ratio of *9 : 3·8* further generations gave a mixture of definite *3 : 1* ratios together with others varying from

* Three families of a later crop have given about the same degree of repulsion.

9 : 5·3 to *9 : 6·4*. Both factors must have been segregating in the original *9 : 3·8* family and the very wide deviation from a *9 : 7* ratio was no doubt due to the repulsion of both factors as already described.

Eleven families, comprising 7,617 plants, have given such abnormal ratios, ranging from *9 : 3·8* to *9 : 6·4*. These may be compared with the following ratios calculated on the assumption that both factors are repelled to the same degree :—

				Black		*Straw*
3	:	*1*	*partial repulsion gives*	*9*	:	*6·06*
7	:	*1*	,, ,,	*9*	:	*4·79*
15	:	*1*	,, ,,	*9*	:	*3·95*

This partial repulsion of ripening black factors may be compared with the total repulsion, already described, of purple stigma and axil by the same internode lining factor. It is of interest, in connexion with theories regarding gametic reduplication in general, that, in certain cases, total repulsion between purple lining and purple stigma was recorded in the same families as were giving the partial repulsion described above.

(*j*) Red rice.

In the process of husking the inner glumes are removed from the *paddy* leaving the *rice* grain free. The colour of this unpolished rice varies in different varieties from clear white, through various subdued shades of cream, yellow, reddish-brown, etc., to the deep red of ordinary *red rice* (Plate V, fig. 1). A still deeper shade, dark blackish-purple, also exists, but has been noted in only one or two varieties of which crosses have not yet been examined.

The colour is contained entirely in the pericarp which is largely removed in the process of polishing to which the rice is submitted before being cooked. Red rice is generally disliked as the polished rice still possesses streaks of red colour in the furrows unless it is very thoroughly polished, in which case the loss of weight and labour entailed are considerable.

Many families segregating for the ordinary *full-red* colour have been examined and, with the exception of a few cases to be considered later, this character has proved to be a simple dominant, due to the presence of a single factor, irrespective of any lighter colouring that may be present.

The figures given in Table XIX indicate a very definite *3 : 1* ratio of *full-red* to *light colour*.

1

2

3

4

COLOURS OF RICE.

1. Full-red
2. Grey-brown
3. White

} from No 153, F_2.

4. Light reddish-brown, No. 162.

TABLE XIX.

Red rice, 3 : 1 ratio.

Origin of parent	Reference No.	Full-red	Light colour	
Sadai Samba × *Boru Murathagna Bhatta* } F_1 ..	639	285	111	*white*
	1,003-N	1,203	413	*do.*
	1,004-N	1,263	398	*do.*
No. 639, F_2	1,008-N	946	338	*do.*
	1,010-N	798	244	*do.*
	1,012-N	1,044	392	*do.*
Natural crosses, F_1 & F_2 ..	Twenty-two lots	6,180	2,023	*carying*
Total ..	..	11,719	3,919	
Calculated 3 : 1 ..	..	*11,728·5* :	*3,909·5*	

In the individual families shown in the above table the *light colour* groups were all *white* since the parents, *Sadai Samba* and *Boru Murathagna Bhatta* were white and red respectively. In the twenty-two families shown together the *light colour* groups varied. In some cases the group was uniform, either white or some definitely light shade of red or brown, whereas in other cases two or more types were present in the same group. In all cases they were very definitely distinct from the *full-red* group.

A similar simple *3 : 1* ratio of *red : white* rice has been recorded by Hector[1], McKerral[2], Thompstone[3], and Van der Stok[4].

In certain exceptional cases a definite departure from this simple ratio was obtained.

Two natural crosses possessing red rice gave three definite groups in F_2, *viz., full-red, grey-brown,* and *white.* The *grey-brown* type of colouring was a distinct type which did not occur in any of the families of Table XIX. The ground-colour was a dull light grey and over this a distinct brown appeared in small scattered spots giving the grain a dingy granular appearance as of white rice rubbed with soil (Plate V, fig. 2). A definite brown line occurred fairly constantly on the ventral edge of the grain.

[1] Hector, G. P., *l.c.*, p. 8.
[2] McKerral, A., *l.c.*, p. 326.
[3] Thompstone, E., *l.c.*, p. 45.
[4] Van der Stok, J. E., *l.c.*, p. 47.

Table XX gives the results obtained in these families with further generations from red-riced parents only as no grey-browns were carried forward.

TABLE XX.

Rice colour.

Origin of parent	Reference No.	Full-red	Grey-brown	White
Natural crosses	822–N	574	206	243
	153–N	72	16	21
No. 153–N, F_2	553–N	315	109	67
	556–N	464	184	150
	562–N	272	81	72
	577–N	340	107	82
No. 577–N, F_3	854–N	650	210	329
	865–N	736	224	189
Total ..		3,423	1,137	1,153
			2,290	
Calculated 9 : 3 : 4 ..	..	*3,213*	*1,071* :	*1,428*
,, *9 : 7* ..	..	*3,213* :	*2,499*	
No. 153–N, F_2	569–N	674	234	..
No. 577–N, F_3	855–N	908	337	..
	858–N	1,018	331	..
	859–N	1,313	266	..
	860–N	813	348	..
	861–N	905	335	..
	862–N	843	289	..
Total ..		6,474	2,140	
Calculated 3 : 1		*6,460·5* :	*2,153·5*	

** To nearest whole figure.*

In the upper half of the table, where all three groups are present, all the families, in spite of some irregularity, show a definite tendency to a *9 : 7* ratio of *full-red : grey-brown+white*, and the totals approximate fairly nearly to this ratio. In the lower half, where white is absent, the ratio *full-red* : *grey-brown* is undoubtedly *3 : 1.*

It would seem from this that in these families the production of full-red is due to the simultaneous presence of two factors, one of which, by itself, produces the grey-brown type. In this case the three groups should show a *9 : 3 : 4* ratio but the actual figures obtained are not very near to this. The ratio of *grey-brown* to *white* varies considerably in the different families and for this reason it is hardly legitimate to total them together.*

A red-riced plant, No. 617-N, from an F_2 family that was segregating but not counted, gave in F_3 *full-red* 949 : *white* 753, a very definite *9 : 7* ratio. Twenty-four segregating F_4 families showed an extraordinary range of ratios, mostly varying from *9 : 3·3—9 : 5·9* but with a few approximating to *9 : 7*. These ratios recall strongly the set of similarly varying ratios obtained in connexion with the ripening black character, where there was evidence that it was due to partial repulsion of the two determining factors by another factor. It appears highly probable that the present case is due to a similar phenomenon.

Two plants in No. 617-N possessed slight reddish rice, quite distinct from the full-reds, and proved to be natural crosses since their progeny contained golden-glumed plants though this character was absent from the original family. When the rice of these two families was examined it was found to vary from definite slight reddish to pure white. This variation was so gradual, as is usual in families segregating for this type of colouring, that definite groups could not be separated, but in both cases all plants with golden glumes possessed pure white rice. An exactly similar result was seen in a totally unrelated family arising from a similar cross in another group. There can be no doubt that in these three families some form of gametic reduplication was taking place in which the factor or factors determining light reddish rice were concerned. This fact supports the supposition that the varying ratios of the families derived from No. 617 were due to gametic reduplication.

The whole question will be carefully followed up, using selfed seed only and noting all segregating characters in connexion with rice-colour. Attempts will also be made to produce red-riced plants by crossing *white* and *grey-brown*, in the case of the 153 group, and different *white* plants in the 617 group. Should both the above types of *9 : 7* ratio be confirmed it would follow that red rice may be due to the simultaneous presence of two factors of which at least one may vary.

With regard to the various light shades of red, brown, etc., it has proved very difficult to obtain definite results. Many families undoubtedly showing

* In the light of later evidence, see Postscript, this view is probably incorrect. [F. R. P.]

segregation have been examined, but, with only one exception, it has been impossible to separate them into distinct groups without all stages of intermediates.

The exceptional family resulted from a naturally occurring heterozygous plant, No. 162, with light reddish-brown rice (Plate V, fig. 4). In F_2 the same type appeared together with pure white. The groups, which were absolutely distinct, showed the ratio *light reddish-brown* 109 : *white* 42, presumably representing a *3 : 1* ratio indicating the simple dominance of this character.

COIMBATORE,
February 14, 1917.

POSTSCRIPT.

Since this paper was written a careful examination has been made of a later crop comprising a number of F_4 families from No. 553, F_3 of Table XX. When the character of the rice was noted in conjunction with other segregating characters it was seen that all *red-riced* plants were *purple-pigmented* whereas all plants with *grey-brown* rice were *unpigmented*.

Table XXI gives the numbers for five families showing segregation for both pigmentation and rice colour. It will be seen that a very definite *9 : 3 : 3 : 1* ratio results from a *3 : 1* ratio of *pigmented : unpigmented*, together with a *3 : 1* ratio of *red : white* in the former group and of *grey-brown : white* in the latter group.

TABLE XXI.

Origin of parent	Reference No.	PURPLE-PIGMENTED		UNPIGMENTED	
		Red rice	White rice	Grey-brown rice	White rice
No. 553-N. F_3 ..	775-N	612	220	226	53
	776-N	400	131	130	46
	777-N	391	147	116	43
	781-N	682	220	235	68
	782-N	450	135	146	50
Total ..	..	2,535	853	853	260
Calculated 9 : 3 : 3 : 1	..	*2,532* :	*844* :	*844* :	*281*

Other families from the same parent gave a simple *3 : 1* ratio of *pigmented, red rice : unpigmented, grey-brown rice* and further analysis of some of the families given in the second half of Table XX shows that the same occurred there.

The most simple and probable explanation of this is that a single red rice factor is concerned, and that this is only able to produce the full-red colour in the presence of the particular purple pigmentation factor that is segregating in this group ; in the absence of this pigmentation factor the red rice factor gives grey-brown.

The existence of unpigmented varieties with red rice would be explained on the assumption that they lack the other of the two pigmentation factors which have already been shown to exist. If this theory is correct crosses between unpigmented red-riced varieties and the above grey-brown type should give a pigmented red-riced F_1, and F_2 should show segregation for both pigmentation factors. This will be tested in due course.

It was found that, owing to the rice-colour not developing properly till the grain is dead ripe, it was better to note this character in the field, leaving each plant till it was absolutely definite, rather than to take one head from each plant when the crop was ripe. The latter method no doubt accounts for much of the irregularity of the numbers in Table XX.

F. R. P.

June, 1917.

PLATE I.

Photographs of Ripe Grains.

1 Long Outer Glumes, "Rakki Pakshi Bhatta."
2-6 Short ditto.

Colours of Inner Glumes.

2 Green, ripening straw, "Poombalai."
3 Dark Gold, "Ponkambi Samba."
4 Dark Furrows, "Shiyali Kar."
5 Piebald Gold, "Garudan Samba."
6 Piebald Dark Furrows, "Manawari."

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